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LARVAL RELEASE RHYTHM COINCIDING WITH SOLAR DAY AND TIDAL CYCLES IN THE TERRESTRIAL CRAB *SESARMA*—HARMONY WITH THE SEMILUNAR TIMING AND ITS ADAPTIVE SIGNIFICANCE

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ABSTRACT

This field study determined which cycle of a lunar day or tide coincides with the time of day of larval release in the terrestrial crab, *Sesarma haematocheir*. Observations of larval release were made at a riverside 100 m upriver from Kasaoka Bay in the Inland Sea of Japan where the tidal phase differs by several hours from that of the Pacific Ocean. The findings demonstrated that the timing of larval release coincided not with a lunar day cycle but with a local tidal cycle. The larval release pattern of the Kasaoka population showed a relatively strong correlation with tides when compared with the Izu population. This suggests that the Izu population pattern was transitional, going from a combined solar day and tidal pattern to a complete daily rhythm. The timing of incubation and larval release may be based on the following mechanisms: semilunar timing of incubation entrained by lunar cycle, and the time of day of larval release controlled by a combination of solar day and local tidal cycle. This study presents further evidence that the semilunar rhythm of incubation and larval release plays an important role in the survival of larvae.

INTRODUCTION

In intertidal zones and estuaries, tidal cycles as well as light and temperature are important physical parameters. The ebb and flow of tides periodically cause drastic changes in the environment, *e.g.* fluctuations of salinity and emersion and submersion of mud flats. These changes, interacting with daily light-dark cycles and seasons, produce complex temporal situations. Under such conditions, each species evolves the means for adequate adaptation for survival and reproduction. Accordingly, behavior and physiology of many organisms inhabiting intertidal and estuarine environments correspond to predictable environmental fluctuations: the daily light-dark cycle, lunar and tidal phases, and seasons, thus showing cyclicity. Also, although considerable information has accumulated on semi-monthly cycles of reproductive activities (Korringa, 1947; Naylor, 1976), little is known about timing mechanisms except for a semilunar rhythm of emergence in the intertidal midge *Clunio* (Neumann, 1966, 1976, 1978).

The purpose of this study is to elucidate the complex timing of egg production and larval release in the terrestrial crab *Sesarma haematocheir*. An overt semilunar hatching rhythm in this species has already been reported (Saigusa, 1980b, 1981). From its habitat, it is supposed that this semilunar rhythm might be induced by a lunar cycle; thus, male and female crabs were exposed to a simulated lunar cycle

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consisting of a 24 h light-dark cycle and a 24.8 h artificial moonlight cycle in the laboratory. This treatment brought about a semilunar rhythm of incubation and larval release (Saigusa, 1980a). The question thus arises: is the time of day of larval release also correlated with the lunar cycle? (If so, it probably corresponds to a range of moonrise time extending from full moon to the last quarter and moonset time from a new moon to the first quarter.) In other words, is the larval release pattern observed in the field (Saigusa, 1980b, 1981) a combination of a 24 h solar day and 24.8 h lunar day or a combination of a solar day and a 24.8 h unimodal tidal component?

A few investigators have presented evidence that the fiddler crab *Uca* also exhibits a semilunar rhythm of larval release (Christy, 1978; Wheeler, 1978). It

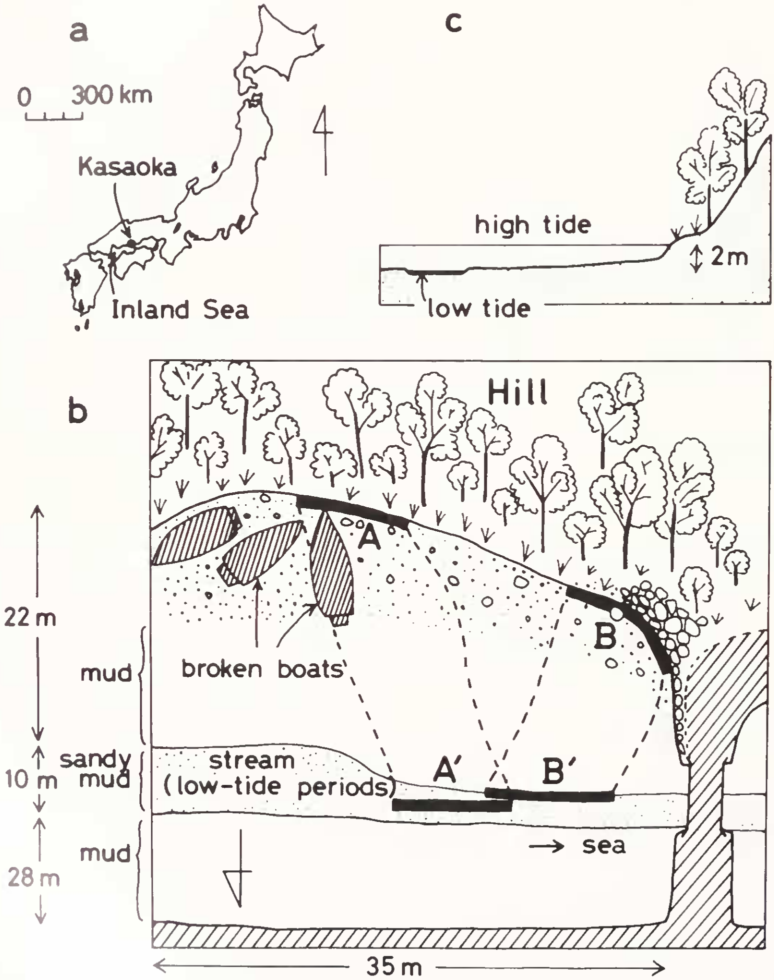

FIGURE 1. Larval release by *Sesarma haematocheir* females was observed at a point 100 m upriver from the Kasaoka Bay in the Inland Sea. Figure 1a shows the location where field work was carried out, and Figure 1b, the environment of the study area. From 11 July to 1 August 1980, site A–A′ was used for observation, and site B–B′, from 1 to 17 September 1980. Figure 1c shows a cross section of the study area.

FIGURE 2. *S. haematocheir* female behavior following larval release. On the final day of embryonic development, egg laden females appear on the riverside to release their clutches at the water's edge. Holding onto stones or rocks, the females vigorously vibrate their abdomens, causing the egg membranes to break, and newly hatched zoeae to emerge.

might be worth while to look for adaptive meaning of such behavior as biological rhythm in *Uca* and *Sesarma* spp. Based on field observations of time of larval release by *S. haematocheir, Sesarma intermedium*, and *Sesarma dehaani* and experiments on the tolerance of zoeae to fresh water, concluded that the semilunar rhythm of larval release gives larvae the best chance for survival (Saigusa, 1981).

The most important point supporting this conclusion is that larval release is concentrated within a few hours after high water occurring about dusk. This poses a problem of tidal synchrony. On coasts with semidiurnal tides, the times of high and low waters on days of full and new moons have occurred at nearly the same time of day for years, but differed depending on the seashore location. (For example, on coasts of the Izu peninsula, the time is around sunrise and sunset for spring tides, but from five to six hours later in the Inland Sea.) Thus the question arises as to whether timing of larval release coincides with local tidal cycles.

The two questions above may be condensed into the following problem: is the time of day of larval release correlated with tidal cycles? To solve this problem,

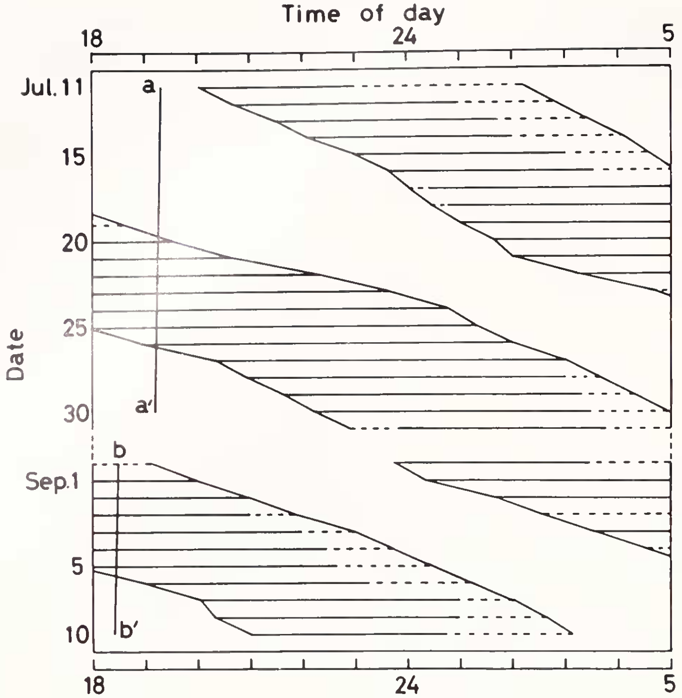

FIGURE 3. Temporal patterns of emersion and submersion on the mud flat of the study area at Kasaoka. Solid lines indicate the time from the beginning to the end of tidal influence. Dotted lines show periods at which tidal data were not obtained. Lines *aa'* and *bb'* connect the sunset times.

a river flowing into the Inland Sea was chosen for observation. On the coasts of the Pacific Ocean including the Izu peninsula, the time of moonrise and moonset is close to that of high water, so that it is very difficult to determine whether the time of day of larval release coincides with the lunar day or tidal cycle.

This paper reports the larval release rhythm of *S. haematocheir* observed at Kasaoka, Okayama Prefecture, Japan. The causes are presented for the difference in the larval release patterns between the Kasaoka population and the Izu population, along along with the timing mechanism of incubation and larval release. The relation of larval release rhythm to local tidal conditions is new evidence for the adaptive significance of semilunar reproductive rhythm in estuarine crabs.

MATERIALS AND METHODS

Larval release by *Sesarma haematocheir* females was observed in Kasaoka, Okayama Prefecture, from 11 July to 1 August, and from 31 August to 17 September 1980. A riverside area located about 100 m upriver from the Inland Sea was chosen as the study site (Fig. 1). The number of females releasing larvae was counted by an electric torch with six 1.5 V batteries. From 11 July to 1 August, a 7–8 m range along the water's edge (site A–A') was observed, but from 31 August to 17 September, about a 10 m range (site B–B') was used. Because a boat at A–A' often hindered observation, the site was moved somewhat in September.

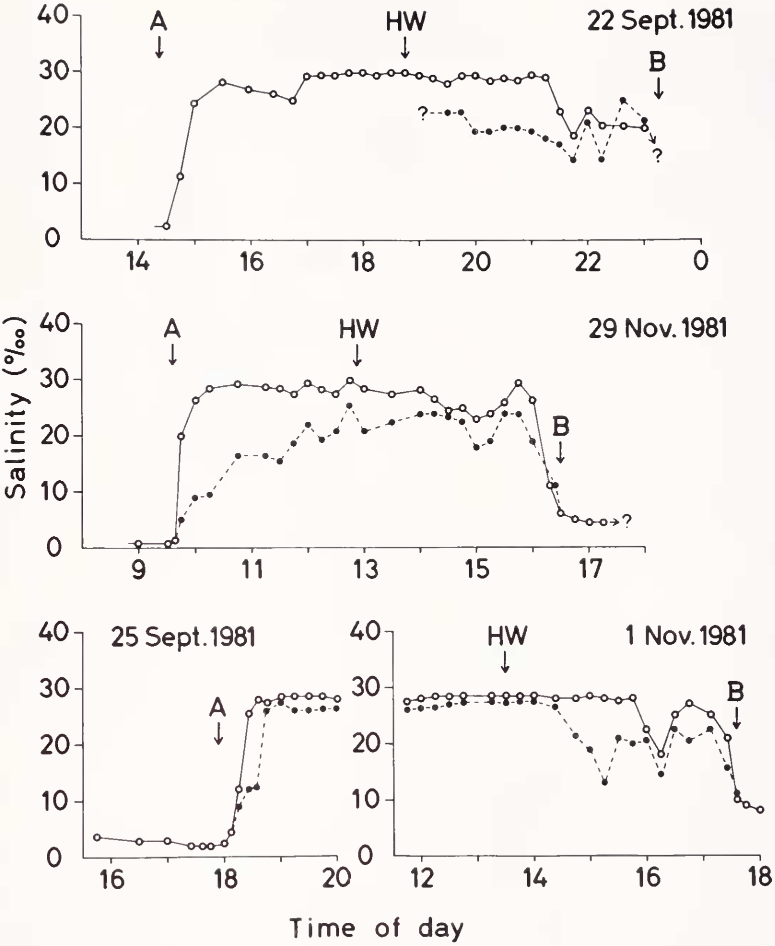

FIGURE 4. Periodic fluctuations of salinity coinciding with tidal cycles at Kasaoka. *A* and *B* show the beginning of a rising tide and the end of a receding tide, respectively. *HW* indicates the time of high water. The upper diagram gives data for the neap tide, the middle diagram data around the spring tide, and the lower diagram data for the spring and neap tides. Dark circles represent salinity at the water's edge (*i.e.*, the surface of water), and open circles indicate the salinity of the river flat at a few meters from the water's edge.

Most females released larvae at the water's edge at either the A or B site. However, within one or two days near the first or last quarter of the moon, the larvae were released at low water or at the receding tide in the middle part of the river.

Most females released larvae while holding onto stones at the water's edge (Fig. 2), but some entered the water to release them on the submerged mud flat. The water was not clear and prevented direct observation of larval release by the females which had moved into deep water. These females returned to the water's edge following larval release and thus were included in the number of females releasing larvae.

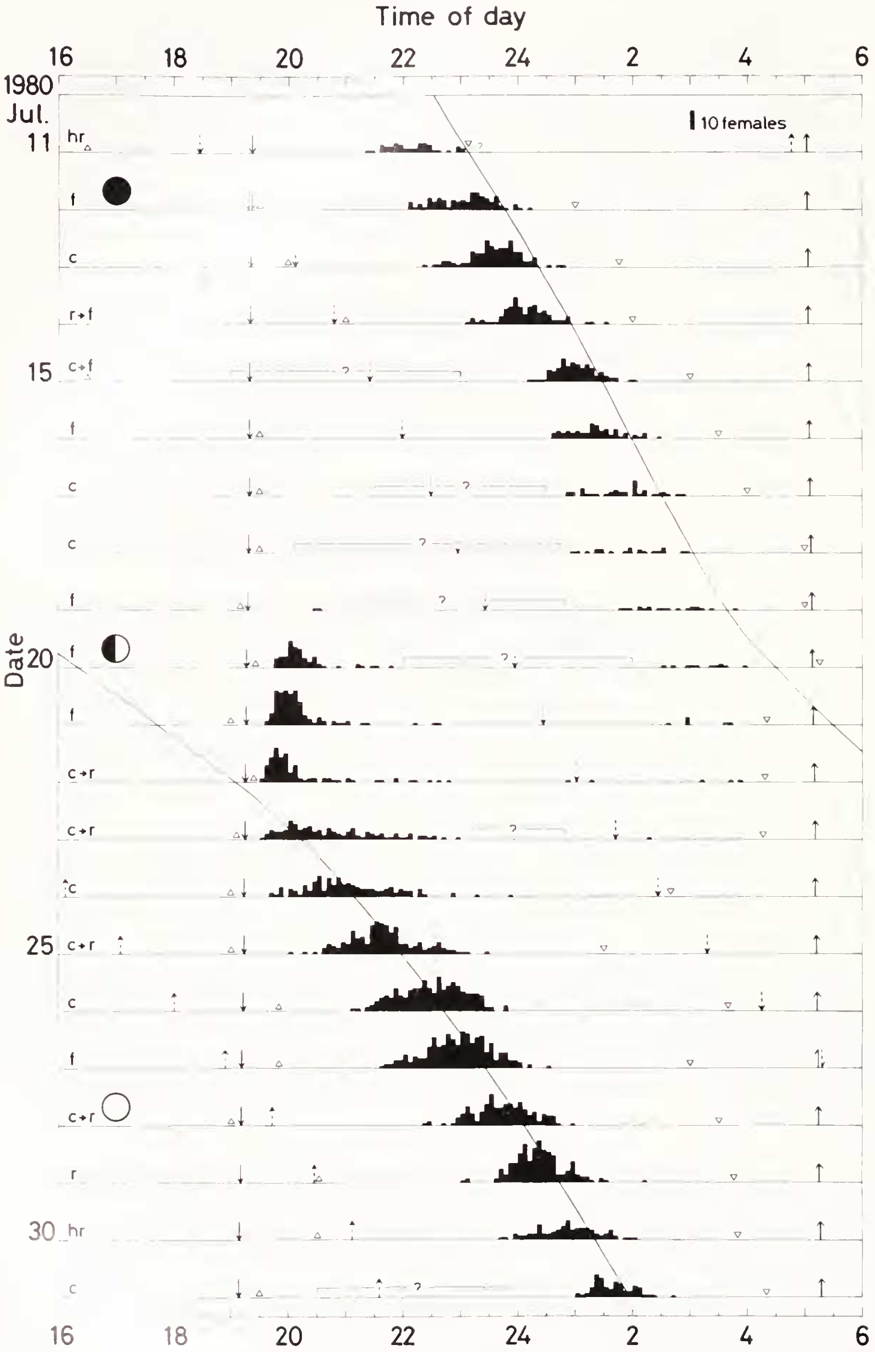

FIGURE 5(A): *S. haematocheir* larval release rhythm at Kasaoka 11 July to 1 August 1980. The number of females releasing larvae per five minutes is expressed in the data. The upward and downward solid arrows represent sunrise and sunset times, respectively. The upward and downward broken arrows show moonrise and moonset times, respectively. The solid diagonal lines connect the high water times, *i.e.*, when the river reached maximum depth. The tidal data were based mostly on the survey, and partly on the tide table. Weather during the observations: fine (f), cloudy (c), rain (r), heavy rain (hr). Question

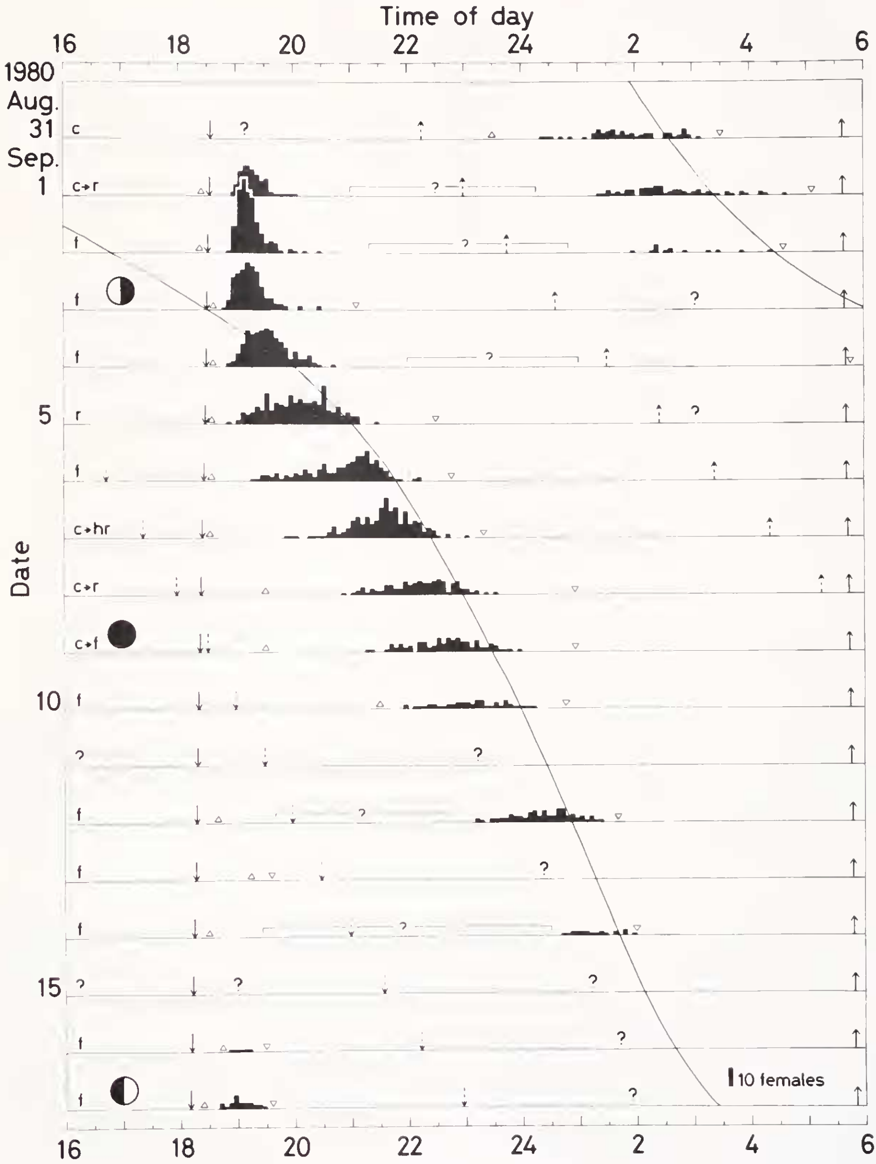

FIGURE 5(B): *S. haematocheir* larval release rhythm at Kasaoka, 31 August–17 September 1980. Symbols are the same as in Figure 5A.

RESULTS

Tidal conditions at Kasaoka

The time of sunrise and sunset on the Inland Sea comes only 18 ± 1 min later everyday, but the tidal phase comes 5–6 h later when compared with the coasts

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marks indicate the day or time when observations could not be made. Beginning and end of observations are shown by upward open triangles (△) and downward open triangles (▽), respectively. The dark and open circles represent new and full moons, respectively. Semicircles, the first or last quarters of the moon.

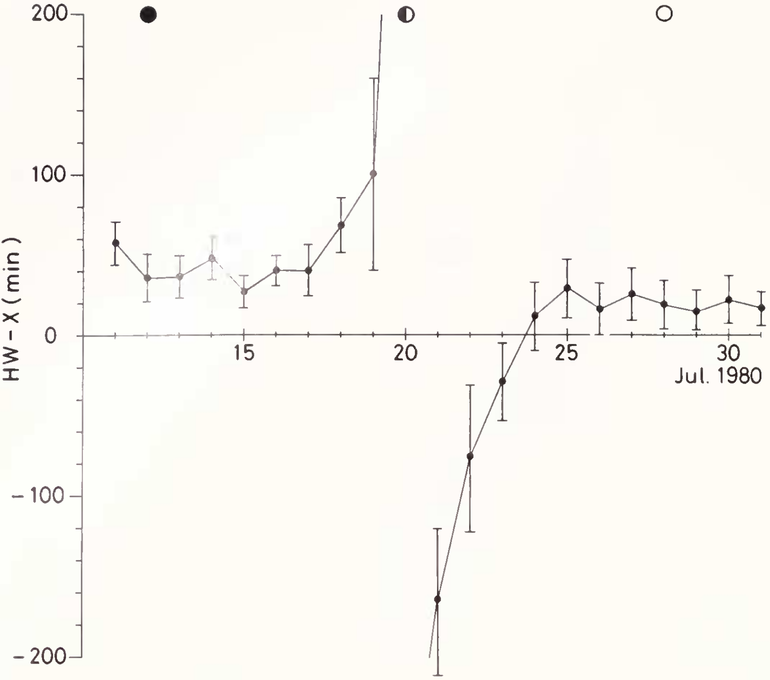

FIGURE 6(A): Correlation between the timing of larval release by the Kasaoka population and the time of high water, 11–31 July 1980. The estimated time from the average peak of the larval release activity ($\bar{X}$) to the time of high water (HW) is plotted. *HW* indicates the time of high water with which larval release coincided. Temporal variation in larval release activity is indicated by standard deviation. Though a nighttime period virtually extended two days, larval release from 24:00 till dawn is included on the date preceeding the actual date.

of the Izu Peninsula. Thus, high water in Kasaoka occurs about noon and midnight at the spring tides and around sunrise and sunset at the neap tides.

In this study site, the river flat emerged at the low water periods, when the river became 5–6 m wider and about 5 cm deeper. The entire estuarine flat was submerged during the high water periods, when the maximum depth of the middle part of the river was recorded at night to be 2.5 m in July and 2.2 m in September. Although few measurements were made of the daytime high water, the tide table indicated that the water level during summer was always lower at the daytime high water than at the nighttime high water, and that the difference between them was 30–50 cm at the spring tides. The water level at the neap tides was recorded at 1.5–1.8 m in the morning and evening high-water periods. Though some difference could be seen in the water level at the high water periods according to the season and lunar phase, it had relatively little influence on the period of emersion and submersion of the mud flat (Fig. 3).

Salinity changed remarkably with ebb and flow of the tides. Also, at high water periods, a considerable difference in salinity was often recorded between water edge or surface and a place where the water was somewhat deeper. The periodic fluctuations in salinity showed a similar pattern in spring and neap tides (Fig. 4).

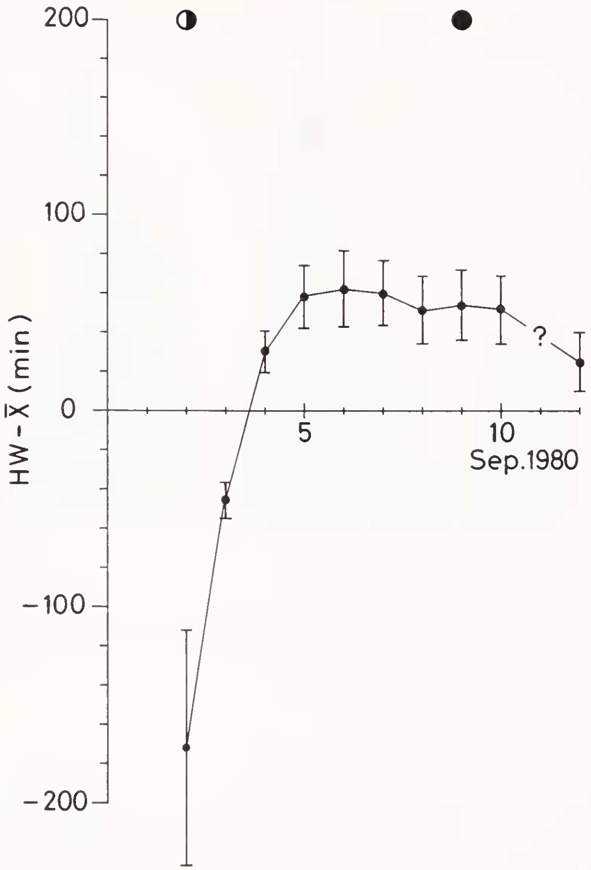

FIGURE 6(B): Correlation between the timing of larval release by the Kasaoka population and the time of high water, 1–12 September 1980. The value for HW-X̄ was calculated by the same method shown in Figure 6A.

Semilunar rhythm of larval release at Kasaoka

The time of day of larval release at Kasaoka is shown in Figure 5. It is evident that the time of day of larval release did not coincide with a lunar day cycle, but with a local tidal cycle. Larvae were released only at night, suggesting that the solar day cycle suppressed daytime larval release in all cases. In addition, larval release activity revealed a combined pattern of 24 h solar day and 24.8 h unimodal tidal components, corresponding to the phase relationship between a solar day cycle and 12.4 h tidal cycle. The solar day component appeared when high water came about sunset and sunrise, and the tidal component appeared at different times.

When the larval release activity revealed a strong correlation with nighttime high water, the average activity peak (X̄) was a little before the high water (HW) (Fig. 6A, B). The estimated time from X̄ to HW then differed somewhat in tidal cycles during the night: 42 min from 11 to 17 July, 17 min from 24 to 31 July, and 49 min from 4 to 12 September, respectively on the average. The average peak

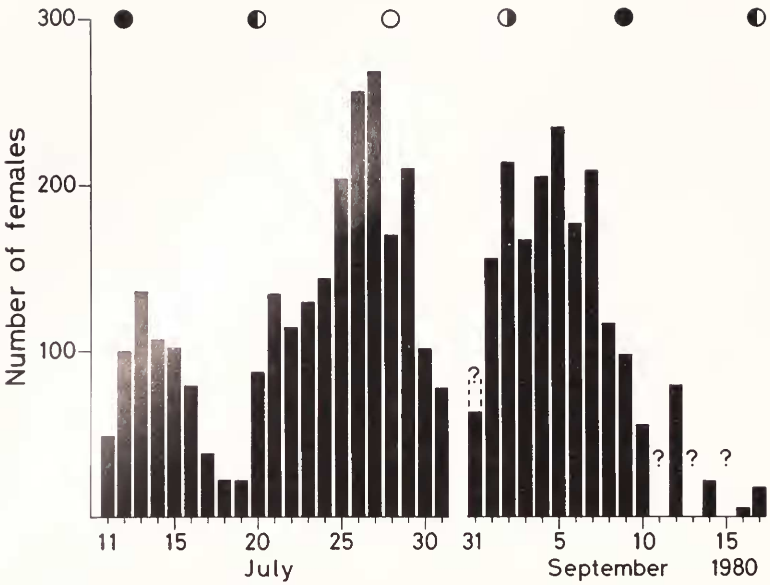

FIGURE 7. Fluctuation in the number of females releasing larvae during the night 11–31 July and 31 August–17 September 1980. Females releasing larvae from 24:00 till dawn are included on the date preceeding the actual date. The open circle indicates a full moon, the dark circles, new moon, and the semicircles, the first and last quarters of the moon.

showed less correlation with tides as the time for high waters approached dawn and sunset, *e.g.* 18 to 20 July (Fig. 6A).

Fluctuation in the number of females releasing larvae every night is shown in Figure 7. Larval release activity in July was semilunar, peaking on the day following the new moon on 12 July and on the day before the full moon on 28 July. More females were seen during the several days close to the full moon than during the new moon. At about the last quarter in September, many females released larvae just after sunset (Fig. 5B), so that larval release activity in September was higher near the last quarter than near the new moon with respect to the lunar phase.

Comparison of larval release patterns between the Kasaoka and Izu populations

Figure 8 shows the *S. haematocheir* larval release rhythm at the Izu peninsula (data from 8 to 24 September 1976). The most remarkable difference between the Kasaoka and Izu population patterns (Figs. 5A, B) is the correlation with the nighttime high water: while the Izu population larval release correlated only weakly with the high water for several days (Fig. 9), the Kasaoka population larval release had a relatively strong correlation with it.

Another difference is the variation in timing of larval release according to the phase relationship between solar day and tidal cycles. While standard deviation in the Izu population activity was very small at times when the afternoon high water came 1–3 h before sunset, that of the Kasaoka population was quite large. In contrast to this, standard deviation in the Izu population timing gradually increased as the high water on one occasion approached midnight, while that of the Kasaoka population was about constant.

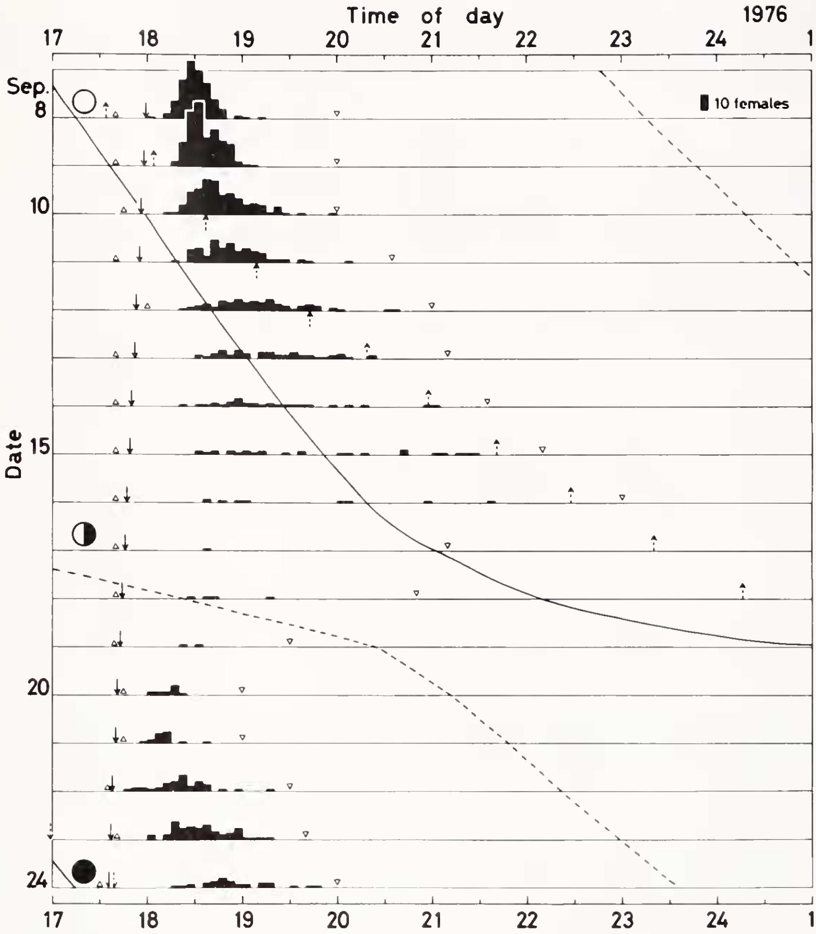

FIGURE 8. *S. haematocheir* larval release rhythm observed at a point 1.5 km upriver from the Pacific Ocean, 8–24 September 1976. The solid and broken diagonal lines connect the times of high water and low water occurring on the seacoast, respectively. These times are not based on the survey but on the tide table in 1976. Other symbols are the same as in Figure 5A.

Standard deviation in each local population was considerably smaller at syzygy, and became larger around a half moon. This is interpreted as an apparent correspondence to the lunar phase, since tidal phase at Kasaoka shifted about 180°, compared with the Pacific Ocean.

DISCUSSION

Larval release rhythm with solar day and unimodal tidal components

For organisms having a semilunar reproductive periodicity, the time of day of reproduction may be divided into two periods with respect to environmental cycles: timing coinciding with a solar day cycle, *e.g.* emergence of the intertidal midge *Clunio Marinus* (Neumann, 1966, 1976) and the sublittoral midge *C. balticus* (Heimbach, 1978), and timing coinciding with either semidiurnal tide, *e.g.*

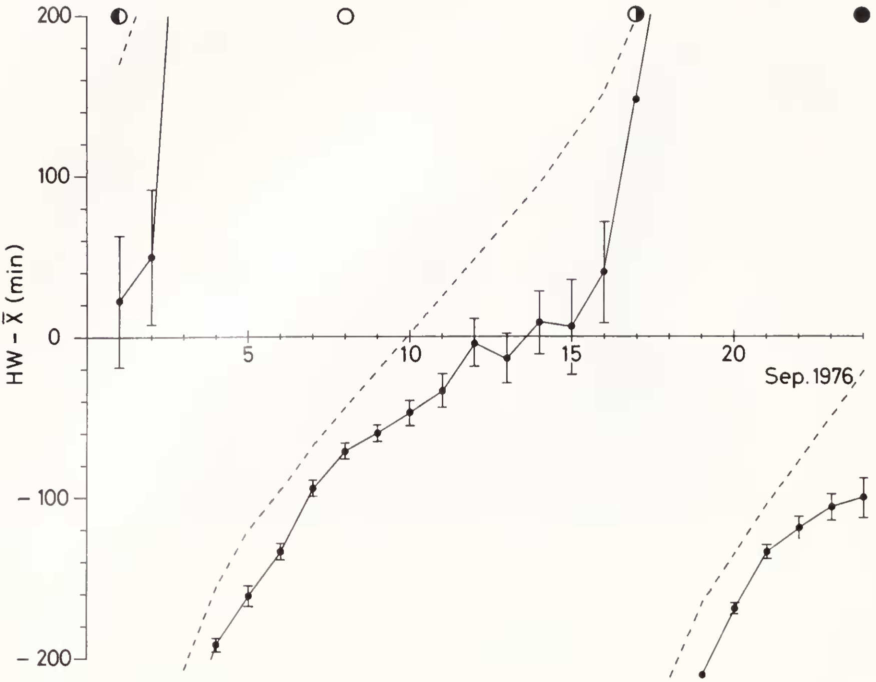

FIGURE 9. Correlation of the timing of the Izu population larval release with high water 1–24 September 1976. The value for HW-X̄ was calculated by the same method shown in Figure 6A. Made from data published elsewhere and Figure 8. Broken lines connect the estimated time from sunset to the high water.

the Japanese midge *C. tsushimensis* (Oka and Hashimoto, 1959) and the grunion *Leuresthes tenuis* (Enright, 1975). In addition, timing coinciding with both solar day and tidal cycles in the *Sesarma* larval release rhythm is reported here.

The combined effects of solar day and tidal components have been described for locomotor activity rhythms of several species of crabs, *e.g. Carcinus* (Naylor, 1958), *Sesarma* (Palmer, 1967) and *Uca* (Barnwell, 1966; Honegger, 1976; Webb, 1976). Whereas locomotor activity usually shows a bimodal tidal component, most reproductive activity seems to be correlated with either semidiurnal tide.

The tidal component was much stronger in the Kasaoka (Figs. 5A, B) than in the Izu population pattern (Fig. 8). This suggests that in the Izu population pattern, the tidal component diminishes. This may be transitional, going from a combined solar day and tidal pattern to a completely daily rhythm.

Two possibilities for the difference in both population patterns are: a direct response to a certain difference in tidal conditions surrounding each population, and population-specific rhythm. Although the study site at the Izu Peninsula was situated at a point near the limit of where tidal amplitude affected the water level, the site at Kasaoka was located only 100 m from the sea. Various influences produced by the tidal cycle would be considerably weakened at a site (Izu) 1.5 km from the seacoast. (For example, tidally correlated vibration would be extremely lessened; and, tidal amplitude might effect the water level only near spring tides.) Therefore, one possibility is that the difference in larval release patterns results from a direct response of females to differences in tidal conditions. Another possibility is that the release is based on population-specific properties. If so, each *S. haematocheir* population would show the same pattern as observed here, at any river site inhabited by this population.

Timing mechanism of egg production and larval release

According to Neumann (1966, 1976), the midge *C. marinus* from southern and middle Europe emerges near daytime low water during a few days at spring tides. He kept cultures of the midge in a 24 h light-dark cycle and then exposed them to a faint light of 0.4 lux a few days each month. This treatment evoked a semilunar rhythm of emergence. In addition, the time of day of emergence followed a 24 h light-dark cycle. He thus demonstrated that the emergence of *C. marinus* is based on a combination of two different timing mechanisms: a semilunar timing of pupation and a daily timing of emergence.

S. haematocheir males and females were exposed to a simulated lunar cycle (Saigusa, 1980a). At first egg production the crabs were divided into three groups: two groups synchronizing with the artificial new moon and one with the artificial full moon (Fig. 7 in *Oecologia* Vol. 46, p. 41). The time from the start of incubation to larval release was about 30 days for each individual; larval release was semilunar. Since nearly all females started the second incubation within a few days, the second larval release also showed semilunar rhythm.

This may be relevant to the field data obtained at the Izu peninusula (Fig. 10): the semilunar rhythm of larval release in the Izu population may also correspond to the three groups of females, *i.e.* two coinciding with the full moon (G-1 and G-3) and one with the new moon (G-2). The peak of larval release on 16 July would have corresponded to the group, G-1, which started egg production near full moon in June. This group would have soon started the second egg production, showing a peak of larval release after 30 days, *i.e.* on 15 August. Moreover, some females might have started the third incubation and released larvae near full moon in September. Another group, G-3, would have started the first incubation near full moon in July, so that the peak of the larval release would have occurred in the next month, on 11 August. This group would have started the second egg production soon, and the peak on 8 September would have corresponded to this group releasing the second clutch. Moreover, another group, G-2, with incubation and larval release coinciding with new moons, would have existed.

This explanation, however, does not account for the inexact correspondence of the semilunar rhythm of larval release to lunar phase. For example, (Fig. 10), though four peaks from August to September have good correspondence with syzygy, peaks on 16 July, 30 July, and 15 August occurred several days after the full and new moons. The Kasaoka population larval release also showed a peak several days before the new moon in September (Fig. 7). These findings might arise from temperature dependency on the period of incubation, or delay or advance of the beginning of incubation from syzygy.

On the other hand, this study presents evidence that the main factors controlling each population's larval release pattern are solar day and local tidal cycles, not the lunar phase. Thus, the timing mechanism of egg production and larval release is interpreted in terms of the following: semilunar timing of incubation and larval release and the time of day of larval release controlled by solar day and tidal cycles.

Adaptive significance of semilunar reproductive rhythm

There are several possibilities for the adaptive function of the semilunar reproductive rhythm exhibited by the fiddler crab *Uca*. For instance, tidal currents

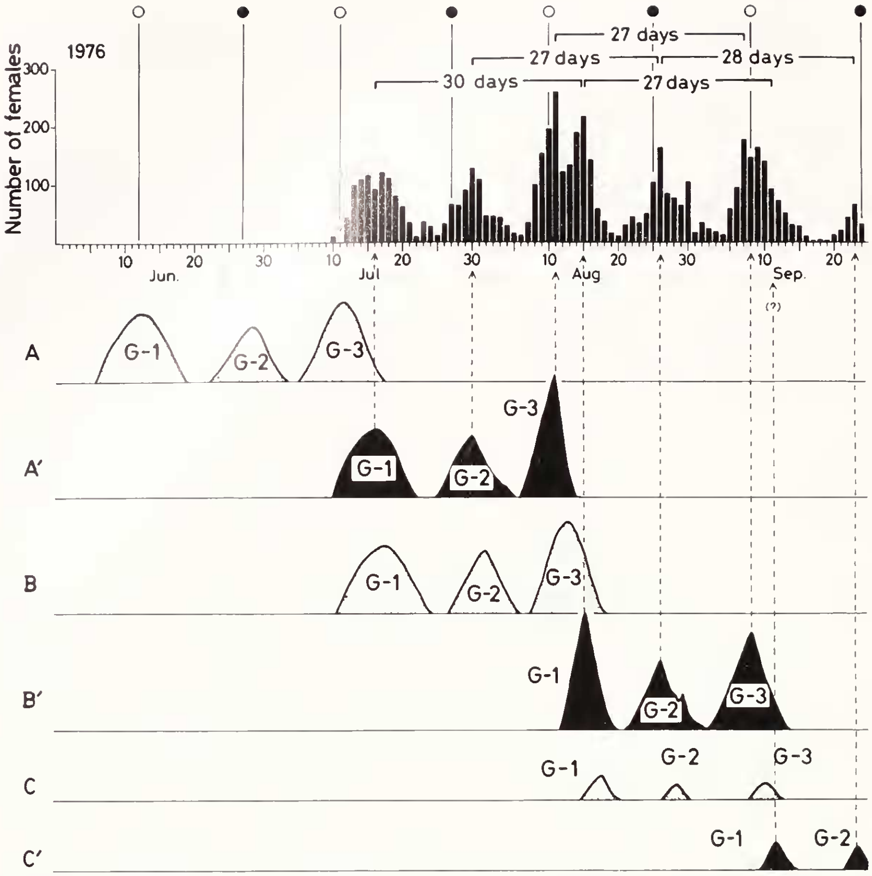

FIGURE 10. Construction of a semilunar larval release rhythm observed at the Izu peninsula in 1976. Results in the laboratory apply to the field data. *A*, the first egg production; *A′*, the first larval release; *B*, the second egg production; *B′*, the second larval release; *C*, the third egg production; *C′*, the third larval release. For further explanation, see text.

associated with high water around full and new moons disperse larvae most effectively in the sea (Wheeler, 1978), and this provides the best opportunity for megalops to be transported to substrates suitable for adults (Christy, 1978; Zucker, 1978).

According to Vernberg and Vernberg (1975), fiddler crab larvae have little tolerance for reduced salinity, though species and seasonal differences exist. The tolerance of *S. haematocheir* and *S. intermedium* zoeae for fresh water is very low, though they are much more resistant of low salinity than *Uca* zoeae. These facts suggest that zoeae released into the river under extremely low salinity conditions might perish.

Salinity at Kasaoka rapidly increased with rising tide, becoming a maximum for a period of six hours when the water was flowing. A comparison of Figure 4 with Figures 5A and B suggests that *S. haematocheir* zoeae are released into the river when the salinity is most favorable: on 20 July (Fig. 5A) and 1 September (Fig. 5B), larvae, released just after sunset, have been exposed to extremely low salinity. At other times, the receding tides carry the larvae to the sea very effectively. Thus, the relation of the semilunar rhythm of larval release to local tidal conditions enhances the probability of larval survival.

For organisms showing semilunar reproductive rhythm, the time of day of reproduction is correlated with either the daytime or nighttime tide. For example, *C. tsushimensis* emerges at the time of daytime low water in summer and nighttime low water in winter (Oka and Hashimoto, 1959). Spawning by *L. tenuis* occurs at high water after sunset (Enright, 1975). *Uca* females apparently release zoeae near high water (DeCoursey, 1979). Larval release by three species of *Sesarma* also occurred at nighttime high water (Saigusa, 1981).

DeCoursey (1979) has suggested that egg hatching at nocturnal high water may minimize predation on egg laden *Uca* females walking to the water's edge to release larvae and also reduce predation on larvae. A special predator on adult and young *Sesarma* is not known as yet. However, schools of the grey mullet (*Mugil cephalus*) were observed entering the rivermouth at rising tide and busily consuming newly released *Sesarma* larvae at the water's edge. This suggests predatory pressure upon larvae at nighttime high water.

The adaptive significance of nighttime larval release by crabs inhabiting estuaries, is obscure. Yet, egg laden females might walk to the riverside by sunset and release larvae.

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LITERATURE CITED

BARNWELL, F. H. 1966. Daily and tidal patterns of activity in individual fiddler crab (genus *Uca*) from the Woods Hole region. *Biol. Bull.* **130:** 1–17.

CHRISTY, J. H. 1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator*: a hypothesis. *Science* **199:** 453–455.

DECOURSEY, P. J. 1979. Egg-hatching rhythms in three species of fiddler crabs. Pp. 399–406 in E. Naylor and R. G. Hartnoll, Eds., *Cyclic phenomena in marine plants and animals.* Pergamon Press. Oxford.

ENRIGHT, J. T. 1975. Orientation in time: endogenous clocks. Pp. 917–944 in O. Kinne, Ed., *Marine ecology, Vol. II, Physiological mechanisms, Part 2.* John Wiley & Sons, London.

HEIMBACH, F. 1978. Sympatric species, *Clunio marinus* Hal. and *Cl. balticus* n. sp. (Dipt., Chironomidae), isolated by differences in diel emergence time. *Oecologia (Berl.)* **32:** 195–202.

HONEGGER, H.-W. 1976. Locomotor activity in *Uca crenulata*, and the response to two Zeitgebers, light-dark and tides. Pp. 93–102 in P. J. DeCoursey, Ed., *Biological rhythms in the marine environment.* University of South Carolina Press, Columbia.

KORRINGA, P. 1947. Relations between the moon and periodicity in the breeding of marine animals. *Ecol. Monogr.* **17:** 349–381.

NAYLOR, E. 1958. Tidal and diurnal rhythms of locomotor activity in *Carcinus maenas* (L.). *J. Exp. Biol.* **35:** 602–610.

NAYLOR, E. 1976. Rhythmic behaviour and reproduction in marine animals. Pp. 393–429 in R. C. Newell, Ed., *Adaptation to environment: essays on the physiology of marine animals.* Butterworths, London.

NEUMANN, D. 1966. Die lunare und tägliche Schlüpfperiodik der Mücke *Clunio.* Steuerung und Abstimmung auf die Gezeitenperiodik. *Z. Vergl. Physiol.* **53:** 1–61.

NEUMANN, D. 1976. Adaptations of chironomids to intertidal environments. *Annu. Rev. Entomol.* **21:** 387–414.

NEUMANN, D. 1978. Entrainment of a semilunar rhythm by simulated tidal cycles of mechanical disturbance. *J. Exp. Mar. Biol. Ecol.* **35:** 73–85.

OKA, H., AND H. HASHIMOTO. 1959. Lunare Periodizität in der Fortpflanzung einer pazifischen Art von *Clunio* (Diptera, Chironomidae). *Biol. Zentralbl.* **78:** 545–559.

PALMER, J. D. 1967. Daily and tidal components in the persistant rhythmic activity of the crab, *Sesarma. Nature* **215:** 64–66.

SAIGUSA, M. 1980a. Entrainment of a semilunar rhythm by a simulated moonlight cycle in the terrestrial crab, *Sesarma haematocheir. Oecologia (Berl.)* **46:** 38–44.

SAIGUSA, M. 1980b. Lunar and semilunar rhythms in reproduction. *Aquabiology* 2: (I) 248–254, (II) 372–377 (In Japanese).

SAIGUSA, M. 1981. Adaptive significance of a semilunar rhythm in the terrestrial crab *Sesarma. Biol. Bull.* **160:** 311–321.

VERNBERG, F. J., AND W. B. VERNBERG. 1975. Adaptations to extreme environments. Pp. 165–180 in F. J. Vernberg, Ed., *Physiological ecology of estuarine organisms.* University of South Carolina Press. Columbia.

WEBB, H. M. 1976. Interactions of daily and tidal rhythms. Pp. 129–135 in P. J. DeCoursey, Ed., *Biological rhythms in the marine environment.* University of South Carolina Press, Columbia.

WHEELER, D. E. 1978. Semilunar hatching periodicity in the mud fiddler crab *Uca pugnax* (Smith). *Estuaries* **1:** 268–269.

ZUCKER, N. 1978. Monthly reproductive cycles in three sympatric hood-building tropical fiddler crabs (genus *Uca*). *Biol. Bull.* **155:** 410–424.